On the endemic Sri Lankan genus *Pettalus* (Opiliones, Cyphophthalmi, Pettalidae) with a description of a new species and a discussion of its diversity

Prashant Sharma, Indika Karunarathna and Gonzalo Giribet: Department of Organismic & Evolutionary Biology and Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138 USA. Email: psharma@fas.harvard.edu

Abstract. A new species of Cyphophthalmi (Opiliones) belonging to the Sri Lankan endemic genus *Pettalus* is described and illustrated. Represented in a recent phylogeny of the family Pettalidae, this species was designated *Pettalus* cf. *brevicauda*, but subsequent examination of its morphology and of the type material of *P. brevicauda* indicates that it is a separate species. Characterization of male genitalia and SEM illustrations are included. Information on other morphospecies recently collected in Sri Lanka indicates that the number of species on the island is higher than previously thought.

Keywords: Gondwana, Pettalus thwaitesi, Sri Lanka

A recent phylogenetic study of Pettalidae Shear, 1980 labeled this family of Cyphophthalmi (Arachnida, Opiliones) a "new model Gondwanan taxon," due to its remarkable distribution on nearly all landmasses of temperate Gondwanan origin (Boyer & Giribet 2007). Currently, Pettalidae is the most diverse family within Cyphophthalmi with respect to both numbers of described genera and species. The pettalid genera of New Zealand in particular have received much attention in taxonomic and biogeographical studies (Boyer & Giribet 2003; Boyer et al. 2007a, 2007b). It is therefore ironic that the type genus and namesake of the family Pettalidae is arguably the most enigmatic among Cyphophthalmi. For over a century, only two species—the first originally assigned to the genus Cyphophthalmus-were formally recognized: Pettalus cimiciformis (O. Pickard-Cambridge 1875) and P. brevicauda Pocock 1897. The former species was described from a single male specimen, collected in Pundaluoya, and the latter from an adult male and a juvenile male, collected in an unspecified locality in "Ceylon" (specimens deposited at The Natural History Museum, London). All three specimens, collected in the nineteenth century, feature a peculiar modification of the terminal opisthosomal tergites that form the "tail" characteristic of male Pettalus. These specimens have been recently illustrated and discussed (Giribet 2008).

Subsequent to the original descriptions (O. Pickard-Cambridge 1875; Pocock 1897), Hansen & Sørensen (1904) undertook a redescription of the anatomy of the specimens for their monograph. However, the redescriptions of Hansen & Sørensen (1904) conflict significantly with the original descriptions, possibly because the two species were confused for each other during redescription and one of the specimens illustrated by Hansen & Sørensen (1904) does not coincide with any of the three specimens reported by Pickard-Cambridge or Pocock (see Giribet 2008). Study of the specimens of P. cimiciformis was not resumed until two recent cladistic analyses of the cyphophthalmid genera (Giribet & Boyer 2002) and specifically of the family Pettalidae (Giribet 2003). These specimens are referred to erroneously as P. brevicauda by Giribet (2003; see also Sharma & Giribet 2006) following the redescription by Hansen & Sørensen (1904), as discussed by Giribet (2008).

Following a field expedition to Sri Lanka in 2004, specifically to collect *Pettalus*, researchers formally described a third species (*P. lampetides* Sharma & Giribet 2006) from an older collection of 75 *Pettalus* specimens consisting of eight morphospecies (specimens collected by Claude Besuchet and Ivan Löbl in 1970). These are currently deposited at the Muséum d'histoire naturelle, Geneva. Although *P. lampetides* was not found during the 2004 field expedition, the description included the first published SEM images and illustrations of *Pettalus* genitalia. Moreover, the presence of eyes in Pettalidae was observed and illustrated for the first time in the course of the *P. lampetides* description, which fundamentally changed the understanding of eye evolution in Cyphophthalmi (Sharma & Giribet 2006; see also Boyer & Giribet 2007).

The 2004 field expedition resulted in the collection of an additional six undescribed species of *Pettalus*. Due to its superficial resemblance to the holotype of *P. brevicauda* and to its geographical location, one of these was designated as *P. cf. brevicauda* and was listed in this manner in two studies: a biogeographical analysis of Pettalidae distribution (Boyer & Giribet 2007) and a broader phylogenetic analysis of the suborder Cyphophthalmi (Boyer et al. 2007b), in addition to a recently published book on Opiliones (Pinto-da-Rocha et al. 2007: fig. 2.1a). This species is also currently being used for sperm ultrastructure and eye ultrastructure studies in G. Alberti's laboratory in Greifswald. However, recent examination of these specimens has indicated that *P. cf. brevicauda* is a separate species from *P. brevicauda* in spite of their superficial similarity.

The inclusion of the molecular sequence data of specimens formerly designated *Pettalus* cf. *brevicauda* in multiple published studies, as well as the ongoing ultrastructural studies of sperm and eye anatomy, has made the formal description of this species imperative. Moreover, the significance of Sri Lanka in biogeographical studies of Pettalidae distribution makes the study of *Pettalus* all the more necessary.

METHODS

Abbreviations.—Examined specimens have been deposited in the following institutions: BMNH = The Natural History

SHARMA ET AL.—DIVERSITY IN THE GENUS PETTALUS

Museum, London (UK); MCZ = Museum of Comparative Zoology, Harvard University, Cambridge (USA); MHNG = Muséum d'histoire naturelle, Ville de Genève (Switzerland); MUP = Museum of the University of Peradeniya, Central Province (Sri Lanka).

Three male and three female specimens were examined with a Scanning Electron Microscope (SEM) FEI Quanta 200. The holotype and a female paratype were photographed in dorsal, ventral, and lateral positions using a JVC KY-F70B digital camera mounted on a Leica MZ 12.5 stereomicroscope. A series of images (from 10 to 15) was taken at different focal planes and assembled with the dedicated software package Auto-Montage Pro Version 5.00.0271 by Syncroscopy. The spermatopositor of a male paratype was examined with a compound microscope with Nomarski Interference Contrast optics, and measured with an ocular micrometer. All measurements are given in millimeters unless otherwise indicated. Nomenclature on cuticular ornamentation follows Murphree (1988).

Specimens previously used for DNA extraction are indicated as such among the type material. Molecular sequence data obtained from these specimens are utilized by Boyer et al. (2007b) and Boyer & Giribet (2007). DNA extraction comprised a non-destructive protocol described in Boyer et al. (2005).

Material for comparison consisted of (1) type specimens of *Pettalus lampetides* (MHNG), Sri Lanka, Diyaluma Falls; (2) holotype of *Pettalus brevicauda* (BMNH), Sri Lanka (locality not specified); and (3) holotype of *Pettalus cimiciformis* (BMNH), Sri Lanka, Punduluoya.

TAXONOMY

Family Pettalidae Shear 1980

Type genus.—Pettalus Thorell 1876.

Genus Pettalus Thorell 1876

Pettalus Thorell 1876:469.

Type species.—*Cyphophthalmus cimiciformis* O. Pickard-Cambridge 1875, by monotypy.

Diagnosis.—Small to medium-sized Cyphophthalmi with distinct bilobed opisthosomal tergite in males, forming characteristic "tail." Eyes with a distinct lens present at the base of the ozophore. Chelicera slightly protruding, proximal article with dorsal and ventral crest, and dual cheliceral dentition. Palpal trochanter without ventral process. Lamelliform adenostyle, swollen at the base, in most proximal region of tarsus IV. Spiracles in the shape of an open circle, nearly C-shaped. Males and females lacking anal glands and modifications thereof. Spermatopositor short, with two movable fingers in gonopore complex, long dorsal microtrichia with bases arranged in a "V" and not fused, and short apical and ventral microtrichia. Ovipositor composed of two apical lobes, each bearing several setae, a long terminal seta, and a sensitive process with a multi-branched seta.

Pettalus thwaitesi new species (Figs. 1-28)

Pettalus cf. *brevicauda* Boyer et al. 2007b:2070–2085 *Pettalus* cf. *brevicauda* Boyer & Giribet 2007:337–361



Figures 1–3.—*Pettalus thwaitesi* sp. nov., male holotype (MCZ 78875): 1. Dorsal view; 2. Lateral view; 3. Ventral view.

Pettalus cf. brevicauda Shultz & Pinto-da-Rocha 2007:16, fig. 2.1a

Type material.—*Holotype:* SRI LANKA: *Central Province:* δ , Peradeniya Botanical Gardens (7°15′54″N, 80°35′39″E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ 78875, ex MCZ DNA101227).

Paratypes: SRI LANKA: Central Province: 4 3° (1 dissected for genitalia, 1 used for DNA extraction), 3 9° , same collecting data as holotype (MCZ 78876, ex MCZ DNA101227); 2 3° , 1 9° same collecting data as holotype (MCZ 78877, 78878, 78879, mounted on SEM stubs); 1 3° , 1 9° , same collecting data as holotype (MUP, ex MCZ DNA101227); 1 9° , Peradeniya Botanical Gardens (7°16'21"N, 80°35'36"E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ 78880, ex MCZ DNA101226, mounted on SEM stubs).

Other material studied: SRI LANKA: Central Province: 1 3 juvenile, same collecting data as holotype (MCZ

THE JOURNAL OF ARACHNOLOGY



Figures 4-6.—*Pettalus thwaitesi* sp. nov., female paratype (MCZ 78876): 4. Dorsal view; 5. Lateral view; 6. Ventral view.

DNA101227); 2 3, 2 9, Peradeniya Botanical Gardens (7°16'21"N, 80°35'36"E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ DNA101223); 4 3, Peradeniya Botanical Gardens (7°16'21"N, 80°35'36"E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ DNA101224, preserved for future RNA extraction); 2 juveniles, Peradeniya Botanical Gardens (7°16'21"N, 80°35'36"E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ DNA101225); 4 & (1 used for DNA extraction), 15 9, 6 juveniles, Peradeniya Botanical Gardens (7°16'21"N, 80°35'36"E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ DNA101226); 2 3, 2 9, Peradeniya, 19 January 1976, C. Besuchet and I. Löbl (MHNG, 1 3, 1 9 mounted on SEM stubs).

Etymology.—The specific epithet refers to George H.K. Thwaites, director of the Peradeniya Botanical Gardens in the nineteenth century, who sent the first *Pettalus* specimen to O. Pickard-Cambridge for the description of *P. cimiciformis*.

Diagnosis.-Medium-sized pettalid with distinct bilobed opisthosomal tergite in males (Figs. 1-3, 7, 11), slightly bilobed in females (Figs. 4, 8, 12). Ozophores of type 3 (Figs. 1, 4). Eyes present, incorporated at the base of the ozophore, with a distinct lens (Figs. 2, 5). Chelicera slightly protruding (Figs. 1, 2), proximal article with dorsal and ventral crest (Fig. 13), and dual cheliceral dentition (Fig. 14). Palpal trochanter without ventral process (Fig. 16). First and second coxae of walking legs free, third coxae fused to fourth. Adenostyle lamelliform, swollen at its base, in most proximal region of tarsus IV (Fig. 25). Spiracles in the shape of an open circle, nearly C-shaped (Fig. 15). Sternites 8 and 9 and tergite IX free, not forming a corona analis (Figs. 11, 12). Male and female lacking anal glands and modifications thereof. Spermatopositor short, of microtrichal formula 6-6-8, with two movable fingers in gonopore complex (Figs. 27-29).

Description.—Total length of male holotype (female paratype MCZ 78876 in parentheses) 3.58 (3.47), width across ozopores 1.04 (1.15), greatest width 1.94 (2.02), equally wide on widest part of prosoma and on second abdominal segment (Fig. 1); length-width ratio 1.85 (1.72).

Body orange to reddish-brown (when preserved in ethanol) depending on incidence of light. Body almost entirely covered by a dense tuberculate-granulate microstructure. Anterior portion of prosoma tapering towards the anterior margin where the chelicerae insert (Figs. 1, 4). Eyes present (Figs. 2, 5). Ozophores conical, of type 3 of Juberthie (1970; see a redefinition of the types of ozophores in Giribet 2003) (Figs. 1, 2, 4, 5). Transverse opisthosomal sulci conspicuous (Figs. 1, 4). Mid-dorsal longitudinal opisthosomal sulcus absent (Figs. 1, 4). Posterior end of the opisthosomal region clearly bilobed in males as a result of an extension of tergite IX, which tapers, forming the characteristic "tail" of the genus (Figs. 1-3, 7, 11); tergites VI to VIII clearly concave (Fig. 2). Dorsal and ventrolateral parts of tergite IX covered with a high concentration of setae (scopulae) (Figs. 1, 3, 11). Female posterior opisthosomal region without clear modifications, although slightly bilobed (Figs. 6, 12).

Coxae of legs I and II movable, coxae of legs III and IV fused (Figs. 9, 10). Ventral prosomal complex of male with coxae of legs II and IV meeting in the midline, but coxae I and III not so (Fig. 9). Pore of coxal gland opening between coxae III and IV (Fig. 9). Sternum absent. Gonostome subsemicircular, approximately as long as wide; lateral walls formed by elevated endites of coxae IV. Ventral prosomal complex of female with only coxae II meeting in the midline. Spiracles in the form of an open circle, although almost Cshaped (Fig. 15), opening towards the postero-lateral side. Sternal opisthosomal glands absent. Sternites 8 and 9 and tergite IX free in males and females, not forming a corona analis (Figs. 11, 12). Relative position of sternite 9 and tergite IX of pettalid type, sensu Giribet & Boyer (2002), where the sternite is embedded by the tergite (Figs. 11, 12). Anal plate without modifications, in ventral position in males and females. Anal gland pores absent (Figs. 11, 12).

Chelicerae (Fig. 13) of protruding type, with the dorsal crest clearly visible from above (Fig. 1); relatively slender; with few



Figures 7-12.—*Pettalus thwaitesi* sp. nov.: 7. Ventral view of male paratype; 8. Ventral view of female paratype; 9. Sternal region of male paratype; 10. Sternal region of female paratype; 11. Anal region of male paratype; 12. Anal region of female paratype.

setae. Granulation restricted to the proximal article covering almost the entire surface, but not the most distal portion. Proximal article of female paratype (MCZ 78876) 1.07 long, 0.46 deep, with conspicuous dorsal crest that extends ventrally but without forming a ventral process, and single posterior ventral process. Second article 1.32 long, 0.19 deep, subcylindrical, its widest portion towards the first third of its length; dentition irregular. Distal article 0.27 long, 0.06 deep, with the two types of dentition typical of pettalids (Fig. 14).



Figures 13–17.—*Pettalus thwaitesi* sp. nov.: 13. External view of left chelicerae of male paratype; 14, Detail of dentition of distal cheliceral segment; 15. Spiracle of male paratype; 16. Left palp of male paratype; 17. Trochanter of male paratype.

Palp (Fig. 16) without ventral process in trochanter (Fig. 17); without conspicuous modifications. Length/width (length-width ratio in parentheses) of palpal articles from trochanter to tarsus of holotype [of female paratype in square brackets]: 0.25/0.11 (2.27) [0.26/0.11 (2.36)]; 0.57/0.11 (5.18) [0.55/0.11 (5.00)]; 0.38/0.11 (3.45) [0.40/0.11 (3.63)]; 0.47/0.10 (4.70) [0.45/0.09 (5.00)]; 0.38/0.08 (4.75) [0.41/0.09 (4.56)]; total length 2.05 [2.07].

Legs (Figs. 18–26) with all claws smooth, lacking dentition or lateral pegs. Surfaces of all trochanters, femurs, patellae, tibiae and metatarsi granulated Figs. 18–21). Granulation of all tarsi concentrating in the proximal and dorsal side (Figs. 22–24, 26); in the case of the male tarsus IV, granulation concentrating in the proximal side, below the adenostyle (Fig. 25). Tarsus I with a distinct solea (Figs. 18, 22). Tarsus IV of males not divided, carrying a lamelliform adenostyle, swollen at its base, in most proximal region of tarsus (Figs. 21, 25). Adenostyle typically folded or bent away from the vertical axis (Fig. 25). Tarsus IV of female without modifications (Fig. 26). Spermatopositor (Figs. 27–29) short, typical of pettalids. Microtrichal formula 6-6-8 (one spermatopositor studied). Dorsal side with a group of eight long microtrichia on each side, with bases arranged in a "V" and not fused. Rounded distal margin with six apical microtrichia, and six short microtrichia adjacent ventrally. Gonopore complex with two distinct movable fingers in the shape of curved hooks.

Leg measurements.—Male holotype (MCZ 78875) in mm, length/width (length/width ratio in parentheses): Leg I: trochanter 0.28/0.26 (1.08), femur 0.94/0.24 (3.92), patella 0.48/0.26 (1.85), tibia 0.66/0.23 (2.87), metatarsus 0.35/0.20 (1.75), tarsus 0.69/0.30 (2.30), total 3.40. Leg II: trochanter 0.23/ 0.23 (1.00), femur 0.71/0.22 (3.23), patella 0.45/0.25 (1.80), tibia 0.54/0.24 (2.25), metatarsus 0.32/0.18 (1.78), tarsus 0.59/0.19 (3.11), total 2.84. Leg III: trochanter 0.26/0.25 (1.04), femur 0.68/0.27 (2.52), patella 0.45/0.26 (1.73), tibia 0.42/0.22 (1.91), metatarsus 0.38/0.20 (1.90), tarsus 0.57/0.20 (2.85), total 2.76. Leg IV: trochanter 0.31/0.24 (1.29), femur 0.99/0.32 (3.09), patella 0.59/0.32 (1.84), tibia 0.74/0.32 (2.31), metatarsus 0.39/ 0.25 (1.56), tarsus 0.69/0.22 (3.4), total 3.71.



Figures 18–26.—*Pettalus thwaitesi* sp. nov.: 18. Male right leg I; 19. Male left leg II; 20. Male left leg III; 21. Male left leg IV; 22. Detail of male right tarsus I; 23. Detail of male left tarsus II; 24. Detail of male left tarsus III; 25. Detail of male left tarsus IV; 26. Detail of female left tarsus IV.



Figures 27–29.—*Pettalus thwaitesi* sp. nov.: 27. Total spermatopositor, dorsal view; 28. Dorsal view showing apical microtrichia and movable fingers; 29. Ventral view. Scale bar = $200 \ \mu m$.

Female paratype (MCZ 78876) in mm, length/width (length/ width ratio in parentheses): Leg I: trochanter 0.28/0.24 (1.17), femur 0.89/0.27 (3.30), patella 0.45/0.26 (1.73), tibia 0.59/0.22 (2.68), metatarsus 0.35/0.18 (1.94), tarsus 0.61/0.29 (2.10), total 3.17. Leg II: trochanter 0.26/0.22 (1.18), femur 0.71/0.27 (2.63), patella 0.42/0.26 (1.62), tibia 0.48/0.25 (1.92), metatarsus 0.35/0.19 (1.84), tarsus 0.52/0.17 (3.06), total 2.74. Leg III: trochanter 0.25/0.24 (1.04), femur 0.75/0.29 (2.59), patella 0.45/0.26 (1.73), tibia 0.49/0.27 (1.81), metatarsus 0.37/0.20 (1.85), tarsus 0.51/0.18 (2.83), total 2.82. Leg IV: trochanter 0.31/0.24 (1.29), femur 0.89/0.30 (2.97), patella 0.51/0.31 (1.65), tibia 0.61/0.30 (2.03), metatarsus 0.38/0.21 (1.81), tarsus 0.62/0.19 (3.26), total 3.32.

Variation.—Range of measurements in males (n = 4) and females (n = 5; in parentheses): Body length 3.38–3.58 (3.38–3.60), maximum (and anterior) width 1.80–1.85 (1.96–2.20).

Distribution.—Known only from the type locality.

Remarks.—*Pettalus thwaitesi* is readily distinguishable from *P. lampetides* by its greater size and the tapering of its opisthosomal tergites. The posterior end of *P. thwaitesi* tapers gradually, whereas that of *P. lampetides* tapers more abruptly in the middle of the opisthosoma. Moreover, spermatopositor morphology, specifically the number of short ventral micro-trichia (six in *P. thwaitesi*, two in *P. lampetides*) readily distinguishes the two. *P. thwaitesi* is smaller than *P. cimiciformis* and has a proportionally smaller upturned "tail." Unlike both *P. cimiciformis* and *P. brevicauda*, *P. thwaitesi* has "protruding chelicers" (sensu Giribet 2003) that do not articulate with the anterior margin of the carapace. Phylogenetically, *P. thwaitesi* is sister to an undescribed species collected from the Hakgala Botanical Gardens, also from the Central Province (Boyer & Giribet 2007).

DISCUSSION

Pettalus thwaitesi clearly belongs to the genus Pettalus on the basis of the apomorphic modification of the terminal opisthosomal tergites forming a "tail" shared by the previously described species of Pettalus. In addition, the typically double cheliceral dentition, ozophore type, and male genitalia are in accordance with traditionally defined pettalid synapomorphies. The monophyly of Pettalus and the inclusion of Pettalus thwaitesi have also been demonstrated in multiple molecular phylogenies (Boyer & Giribet 2007; Boyer et al. 2007b).

The description of a second *Pettalus* spermatopositor in the present study recapitulates the usefulness of genitalic morphology in distinguishing closely related species of Cyphophthalmi. Continued study of *Pettalus* diversity should not overlook the taxonomic worth and evolutionary implications of spermatopositor morphology.

Despite the paucity of described *Pettalus* species, at least thirteen morphospecies remain available for description and study. These include (1) the seven morphospecies from the 1970 MHNG expedition, (2) the remaining five from the 2004 MCZ expedition, and (3) one other species collected by S. Mahunka & L. Mahunka-Papp, deposited at the Hungarian Natural History Museum (Budapest). The distribution of these species in a relatively small area suggests significant diversity of cyphophthalmid fauna in Sri Lanka. Due to the small size and leaf-litter habitat of most cyphophthalmid species, it is probable that additional species will be discovered on the island.

ACKNOWLEDGMENTS

This material is based upon work supported by the National Science Foundation under Grant No. 0236871. Fieldwork for this study was supported by a Putnam Award, from the Museum of Comparative Zoology, Harvard University. Collecting permits were facilitated by the Director of the Peradeniya Botanical Gardens through the support of Mangala de Silva. We are indebted to Mark Harvey and two anonymous reviewers for comments on an earlier version of this article. Paula Cushing and Julie Whitman-Zai edited the manuscript for suitability of publication.

LITERATURE CITED

- Boyer, S.L., J.M. Baker & G. Giribet. 2007a. Deep genetic divergences in *Aoraki denticulata* (Arachnida, Opiliones, Cyphophthalmi): a widespread "mite harvestman" defies DNA taxonomy. Molecular Ecology 16:4999–5016.
- Boyer, S.L., R. Clouse, L. Benavides, P. Sharma, P. Schwendinger, I. Karunarathna & G. Giribet. 2007b. Biogeography of the world: a case study of globally distributed arachnids. Journal of Biogeography 34:2070–2085.
- Boyer, S.L. & G. Giribet. 2003. A new Rakaia species (Opiliones, Cyphophthalmi, Pettalidae) from Otago, New Zealand. Zootaxa 133:1–14.
- Boyer, S.L. & G. Giribet. 2007. A new model Gondwanan taxon: systematics and biogeography of the harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi), with a taxonomic revision of genera from Australia and New Zealand. Cladistics 23:337–361.
- Boyer, S.L., I. Karaman & G. Giribet. 2005. The genus Cyphophthalmus (Arachnida, Opiliones, Cyphophthalmi) in Europe: a phylogenetic approach to Balkan Peninsula biogeography. Molecular Phylogenetics and Evolution 36:554–567.
- Giribet, G. 2003. *Karripurcellia*, a new pettalid genus (Arachnida, Opiliones, Cyphophthalmi) from Western Australia, with a cladistic analysis of the family Pettalidae. Invertebrate Systematics 17:387–406.
- Giribet, G. 2008. On the identity of *Pettalus cimiciformis* and *P. brevicauda* (Opiliones, Pettalidae) from Sri Lanka. Journal of Arachnology 36:199–201.

- Giribet, G. & S.L. Boyer. 2002. A cladistic analysis of the cyphophthalmid genera (Opiliones, Cyphophthalmi). Journal of Arachnology 30:110–128.
- Giribet, G., G.D. Edgecombe, W.C. Wheeler & C. Babbitt. 2002. Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. Cladistics 18:5–70.
- Hansen, H.J. & W. Sørensen. 1904. On Two Orders of Arachnida: Opiliones, Especially the Suborder Cyphophthalmi, and Ricinulei, Namely the Family Cryptostemmatoidae. Cambridge University Press, Cambridge, UK. 182 pp.
- Juberthie, C. 1970. Les genres d'opilions Sironinae (Cyphophthalmes). Bulletin du Muséum National d'Histoire Naturelle 41:1371–1390.
- Murphree, C.S. 1988. Morphology of the dorsal integument of ten opilionid species (Arachnida, Opiliones). Journal of Arachnology 16:237–252.
- Pickard-Cambridge, O. 1875. On three new and curious forms of Arachnida. Annals and Magazine of Natural History, Series 4 16:383–390.
- Pinto-da-Rocha, R., G. Machado & G. Giribet (eds.). 2007. Harvestmen: the Biology of Opiliones. Harvard University Press, Cambridge, Massachusetts. 597 pp.
- Pocock, R.I. 1897. Descriptions of some new Oriental Opiliones recently received by the British Museum. Annals and Magazine of Natural History, Series 6 19:283–292.
- Shear, W.A. 1980. A review of the Cyphophthalmi of the United States and Mexico, with a proposed reclassification of the Suborder (Arachnida, Opiliones). American Museum Novitates 2705:1–34.
- Sharma, P. & G. Giribet. 2006. A new *Pettalus* species from Sri Lanka with a discussion on the evolution of eyes in Cyphophthalmi. Journal of Arachnology 34:331–341.
- Shultz, J.W. & R. Pinto-da-Rocha. 2006. Morphology and functional anatomy. Pp. 14–61. In Harvestmen: The Biology of Opiliones. (Pinto-da-Rocha, R., G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Manuscript received 8 July 2008, accepted 15 September 2008.